

EGG DISPERSION PATTERNS AND EGG AVOIDANCE BEHAVIOR IN THE BUTTERFLY *PIERIS SISYMBRII* BDV. (PIERIDAE)

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ABSTRACT. Egg dispersion patterns of the pierid butterfly, *Pieris sisymbrii* Bdv., were studied in the Mojave Desert, San Bernardino County, California. A census of eggs found on its cruciferous hostplant, *Arabis pulchra*, revealed a clumped egg dispersion pattern. This is an unexpected result if females of *P. sisymbrii* avoid conspecific eggs. An egg removal experiment suggested that *P. sisymbrii* females avoided plants bearing eggs, selecting egg-free hosts instead. In times of limited egg-laying sites, extended female flights due to successive rejections of egg-bearing plants may be a cue to inhibit egg-avoidance behavior, causing females to select egg-bearing hosts more frequently.

Ovipositing females of some inflorescence or infructescence-feeding pierid butterflies avoid those cruciferous host plants bearing conspecific eggs. Females which can recognize the presence of conspecific eggs on potential host plants apparently avoid host overload by assessing their egg-load and if necessary, adjusting their oviposition behavior, accepting only plants without eggs (Shapiro, 1980). When sufficient host plants are available, egg-load assessment and egg avoidance behavior should lead to a uniform egg dispersion pattern. Supporting studies have been obtained from laboratory work with *Pieris brassicae* L. (Rothschild & Schoonhoven, 1977), and field work with *Anthocaris sara* Lucas (Shapiro, 1980), *Euchloe hyantis* Edw. (Shapiro, 1981a), and *Anthocaris cardamines* L. (Wiklund & Åhrberg, 1978).

Prevention of host overload is adaptive in that the amount of food plant on a single plant or stem is usually enough for only the first hatched larva, and any subsequent larvae may have little or no food plant available to consume (Rauscher, 1979). Older larvae may also exhibit cannibalistic tendencies toward eggs and younger larvae (Stamp, 1980). When plants free of eggs are available, it would seem maladaptive for assessing butterflies to utilize plants already bearing eggs.

Several investigators, however, have found clumped or aggregated egg dispersion patterns, usually as a consequence of female butterflies utilizing isolated plants or plants found along the margins of host plant clumps (Mackay & Singer, 1982; Cromartie, 1975; Jones, 1977; Courtney & Courtney, 1982). The use of a few isolated plants by females can leave individual hosts with far more eggs than they can support.

The California white, *Pieris sisymbrii* Bdv., is a member of a large group of pierid butterflies that feed preferentially on inflorescences; however, the favorite oviposition sites are on stems and undersides of cauline leaves. In the Mojave Desert, *P. sisymbrii* lays blue-green eggs

on its host plant, *Arabis pulchra* Jones (Brassicaceae). The eggs then turn a conspicuous bright orange within a day. Many assessing pierid butterflies have brightly colored orange-to-red non-cryptic eggs, perhaps to facilitate egg recognition by females (Shapiro, 1981a).

This study examines egg-load assessment and egg avoidance behavior in *P. sisymbrii* in the Mojave Desert. I attempt to answer two questions: (1) Is the initial egg dispersion pattern in the field the expected uniform distribution, and if not, are there explanations for deviations from uniformity? (2) Does *P. sisymbrii* avoid egg-bearing host plants when egg-free plants are available, thus suggesting a discriminatory behavior?

Study Area

The study site consisted of low rolling hills approximately 1000 m in elevation and located 30 km south of Baker, San Bernardino County, California (Mojave Desert). Dominant shrubs include Joshua tree (*Yucca brevifolia* Engelm.) and creosote bush (*Larrea divaricata* Cav.) and their associates. The area supports large populations of crucifers, including *Caulanthus cooperii* (Wats.) Pays., *Descurainia pinnata* Walt., as well as *A. pulchra*. *Arabis pulchra* occurs primarily along washes between adjacent hills. The plant is perennial and may be woody or herbaceous, depending on its age and growing conditions. Its habit is variable; occasionally a single plant may have up to 15 stems while other plants may have only a single stem.

Pieris sisymbrii adults are found in open, exposed areas where solar radiation is high and are most active in the mid-morning (Emmel & Emmel, 1973).

METHODS

A sample of 60 specimens of *A. pulchra* was selected for an egg-removal experiment. Plants were chosen based on the following criteria: (1) High relative conspicuousness; some plants occurred in the center of shrubs, making their inflorescences and flowers difficult to see. These plants were excluded. (2) Plants with only a minimal amount of herbivore damage. No plants with chewed-up leaves or flowers were selected. (3) Satisfactory number of flowers and flower buds. Females may utilize only those plants with a sufficient food resource for the larvae.

All sampled plants were inspected initially for *P. sisymbrii* eggs, and the number of eggs per plant was recorded. Egg color and egg position on the plant were also tabulated. Plants were assigned to a control group and an experimental group. Plants bearing at least one egg were tagged and assigned to the control group, with their eggs left in place.

TABLE 1. Distribution of *Pieris sisymbrii* eggs on *Arabis pulchra* on a per-plant basis.

All eggs		Orange eggs only	
No. eggs/plant	No. of plants	No. eggs/plant	No. of plants
0	23	0	40
1	22	1	15
2	8	2	2
3	2	3	2
4	3	4	<u>1</u>
5	1		60
6	0		
7	<u>1</u>		
	60		

Plants without eggs were tagged and assigned to the experimental group. No apparent morphological differences between egg-free and egg-bearing plants were observed. Thirty-seven plants were initially found to bear eggs, and to simplify the statistics involved, eggs were removed from seven randomly selected control plants, and these plants were added to the experimental group. In this way, each group included 30 plants. Eggs were removed from the plants by teasing with an insect pin and a camel hair brush.

The study site was visited for six consecutive days, 27 March through 1 April 1983. Inspection for newly laid eggs started at 1000 h each day just as butterfly activity was peaking. If new eggs were found on the control plants they were noted and left on the plant; if new eggs were found on the experimentals, they were noted and removed from the plant, as described above. A variance-to-mean ratio (s^2/\bar{x}) was used to measure dispersion patterns.

RESULTS

Sixty-eight eggs were found initially on 37 sample plants, with 15 of these plants bearing more than one egg. Distribution of eggs on a per plant basis appears on Table 1. One individual plant (with a single stem) bore seven eggs, all of which were a few inches from one another.

A variance-to-mean ratio was calculated on a per-plant basis and was significantly greater than one, indicating an aggregated egg distribution (Table 2). This suggests that *P. sisymbrii* was not assessing its egg-load on *A. pulchra*. If egg color is an indication of the age of the egg, females may be avoiding orange eggs only since these would be the first to hatch, and the resulting larvae would have a considerable head start in development. The variance-to-mean ratio for orange eggs only, however, still deviates toward an aggregated distribution, albeit not as extreme a deviation as on a per-plant basis (Table 2).

TABLE 2. Dispersion of *Pieris sisymbrii* Bdv. eggs found on *Arabis pulchra* Jones. Variance-to-ratios (s^2/\bar{x}) were calculated on a per-plant and per-inflorescence basis.

	N	\bar{x}	s^2	$(s^2/\bar{x})^a$	χ^2
Per-plant					
All-eggs	60	1.13	1.98	1.75	103.25 ¹
Orange eggs only	60	0.55	0.73	1.33	78.50 ²
Per-inflorescence					
All-eggs	190	0.36	0.68	1.89	359.10 ³
Orange eggs only	190	0.15	0.24	1.60	302.40 ³

^a Any value $\ll 1$ indicates a uniform distribution; $\gg 1$ indicates an aggregated distribution; \approx indicates a random distribution.

¹ $0.005 > P$; df = 59.

² $0.10 > P > 0.05$; df = 59.

³ $0.005 > P$; df = 189.

Shapiro (1980) suggests that assessment works on a per-inflorescence basis, where multiple ovipositions occur on plants with many stems. Females may perceive individual stems as individual oviposition sites and flowers from single inflorescences as adequate food resource for one developing larva. In such cases, many eggs may be found on multi-stemmed plants. A total of 190 stems were counted from the 60 sample plants (Table 3). The deviation toward an aggregated distribution, however, was the most extreme in this treatment (Table 2). Over 50% of the eggs occurred on stems with at least one other egg.

The result of the egg removal experiment indicates that *P. sisymbrii* prefers to oviposit on host plants without eggs. During the week, 27 new eggs were found on the experimental plants compared with 10 on the controls ($\chi^2 = 7.81$, df = 1, $0.010 > P > 0.005$). This suggests that females can recognize eggs and discriminate against those plants bearing eggs, thus effectively avoiding possible larval competition and increasing larval survivorship.

DISCUSSION

In all treatments, *P. sisymbrii* eggs in the field failed to correspond to the uniform dispersion pattern expected if females show egg-load assessment and egg avoidance behavior. The variance-to-mean ratios based on a per-plant, egg color, and inflorescence basis all deviated toward aggregated egg distributions. Such concentration of eggs on a few host plants has been shown to result in lower larval survival in the papilionid *Battus philenor* feeding on *Aristolochia* (Rausher, 1979). The use of a single stem or plant by many larvae will affect their chances of survival, especially if the amount of foodplant available to an individual offspring is small relative to its food requirements, or if the needed resource is limited by certain age and physiological con-

TABLE 3. Distribution of *Pieris sisymbrii* eggs on *Arabis pulchra* on a per-inflorescence basis.

All eggs		Orange eggs only	
No. eggs/inflor.	No. of inflor.	No. eggs/inflor.	No. of inflor.
0	146	0	169
1	28	1	15
2	12	2	4
3	3	3	2
4	0		190
5	0		
6	0		
7	1		
	190		

ditions, as inflorescences are. Any positive preference for plants bearing conspecific eggs would cause intense intraspecific competition and lowered larval survivorship. Such behavior would be maladaptive and result in a reduced fitness and therefore should not evolve.

Several authors have found that individual host plants along the margins of clumps may receive a disproportionate number of eggs relative to inner plants (Courtney & Courtney, 1980; Mackay & Singer, 1982; Cromartie, 1975; Jones, 1977). Shapiro (1975) suggests that the use of these margin plants would be a selected response to defend against parasitoids which key in on high host plant density. Courtney and Courtney (1982) studied aggregated egg patterns of *Anthocaris cardamines* but did not prove any single factor as causing disproportionate egg concentrations. Several aspects of female behavior, they believe, contribute to the large egg loads on individual margin plants—or the 'edge-effect' as they call it. Such behaviors include (1) a tendency of *A. cardamines* to oviposit on its host plant after flying a long distance, even if conspecific eggs are already present, and (2) a host searching behavior in which females sample plant clumps as if plant density is low or plants are widely dispersed. These behaviors may be adaptive if host plant populations undergo periodic fluctuations in total biomass. The selective disadvantage of laying eggs on plants with conspecific eggs would be counterbalanced by successful discovery of hosts during times of low plant density, with females accepting even those which have conspecific eggs.

At the Mojave site, *A. pulchra* occurred almost exclusively along dry washes where plants were distributed in a linear fashion making it difficult to visualize a margin. Interplant distance was approximately 20 m, implying no true area with a high concentration of plants. This high interplant distance, however, may cause females to perceive in-

dividual hosts as isolated plants, and large egg loads may be expected. Shapiro (1981a) found isolated host plants of *Barbarea verna* (Mill.) Asch. to bear up to 15 eggs of *Anthocaris sara*. Mackey and Singer (1982) found that the probability of *Euptychia libye* L. (Satyridae) ovipositing on a sprig of *Panicum* sp. increased as the spatial isolation of the plant increased. They interpreted their results as being a consequence of random initiation of search pattern by the female after an oviposition period, rather than an active preference for isolated plants. It was difficult to judge if any particular plant at the Mojave site was more isolated than others. All plants, however, were within sight of each other, and no plants were found outside the wash.

Despite the initial aggregated egg dispersion pattern, *P. sisymbrii* preferred to oviposit on host plants free of eggs, according to the results of the egg removal experiment. The experimental plants received 27 new ovipositions within the week compared with 10 on the controls. One experimental plant received a new oviposition on three consecutive days. Two other experimental plants, on the second and fifth day respectively, bore two new green eggs during the day; both were counted as a single oviposition event.

The aggregated egg dispersion patterns and the apparent egg avoidance behavior seem to offer conflicting evidence. Yet, aggregated dispersion patterns need not disprove some degree of egg avoidance behavior (Singer & Mandracchia, 1982). My data is consistent with the selective behavior proposed by Courtney and Courtney (1982) where long flight distances by females could cause them to lose their discriminating behavior and lay more eggs on normally avoided plants. When suitable host plants are sparse due to adverse environmental conditions, such as a flood or drought, females have abnormally long oviposition flights to find the few plants available and ignore any eggs that are present. Therefore, indiscriminate egg-laying behavior after lengthy oviposition flights may be advantageous in habitats with great environmental extremes where the probability of encountering egg-free plants is sometimes low. The consequence of encountering and rejecting egg-laden plants consecutively is an increase in flight time and flight distance. This could be the cue which serves to inhibit assessment behavior and increase the probability of a female accepting an oviposition site that would normally be disregarded.

Possible coevolutionary results of egg-load assessment and egg-avoidance behavior can be seen on a local race of one of *P. sisymbrii*'s northern California host plants, *Streptanthus brewerii* Gray (Shapiro, 1981b). These plants produce pigmented callosities which appear to be "egg-mimics." Females were shown to be more apt to oviposit on plants

which had their callosities removed, thus, suggesting a visual cue for egg avoidance (see also Williams & Gilbert, 1981).

My study assumes that assessment behavior is primarily based on visual cues, although pheromonal ovipositional deterrents have been observed in a butterfly species (Rothschild & Schoonhoven, 1977) and in a few dipteran species (Prokopy, 1975; Zimmerman, 1979) and therefore cannot be ruled out.

Other possible responses exist besides the inhibition of avoidance behavior. In times of limited optimal oviposition sites, females may disperse to another suitable area or choose alternative hosts. Further study is needed to check for any relationships between extended ovipositional flights and the degree of host selectivity by the females. It is suggested, however, that *P. sisymbrii* may avoid those plants bearing conspecific eggs as long as egg-free plants are available as alternatives. Once all or most of the available hosts have been taken, females may cease their discriminatory behavior and oviposit on plants with eggs instead of not laying eggs at all.

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